Seasonal variations in phenological traits: leaf shedding and cambial activity in Parkia nitida Miq. and Parkia velutina Benoist (Fabaceae) in tropical rainforest

Hélène Morel, Thomas Mangenet, Jacques Beauchêne, Julien Ruelle, Eric Nicolini, Patrick Heuret, Bernard Thibaut

Seasonal variations in phenological traits: leaf shedding and cambial activity in *Parkia nitida* Miq. and *Parkia velutina* Benoist (Fabaceae) in tropical rainforest

Hélène Morel · Thomas Mangenet · Jacques Beauchêne · Julien Ruelle · Eric Nicolini · Patrick Heuret · Bernard Thibaut

Abstract

Key message **In French Guiana, the leaf and cambium phenologies should not be considered only as exogenous-driven processes, as the dry season, but also as endogenous-driven, as tree development stage.**

Abstract Studies of the periodicity of wood formation provide essential data on tree age and on factors that control tree growth. The aim of this work was to investigate cambial phenology and its relation with leaf phenology and climatic seasonality in two briefly deciduous tropical rainforest species belonging to the genus *Parkia.* Wood microcores were collected every 15 days from April 2009 to February 2012 from five trees of each species. The microcores were stained with cresyl violet acetate to facilitate counting the number of cells in the cambial zone, in the radial enlargement zone and wall-thickening zone. At the same time, we observed leaf shedding pattern in the crown of the same trees. In both species, cambial activity was significantly reduced during the leafless period. In *P. nitida*, these two concomitant events were observed during the dry season whereas in *P. velutina* they can occur anytime in the year with no apparent link with seasonality. In conclusion, the period of reduced cambial activity in some tropical rainforest trees may be independent of rainfall seasonality and not necessarily follow an annual cycle. It appears that leaf phenology is a good proxy to estimate cambial activity.

Keywords Cambial activity · Tropical rainforest · Climate · Leaf shedding pattern · French Guiana

Introduction

Studies of the periodicity of wood formation provide key data that constitute the basis of dendrochronological

H. Morel (✉)
UAG, UMR ECOFOG, ECOlogie des FOrêts de Guyane, BP 701, Kourou 97387, French Guiana, France
e-mail: helene.morel@cirad.fr

T. Mangenet
INRA, UMR AMAP, botAnique et bioinforMatique de l'Architecture des Plantes, Montpellier, France

T. Mangenet · J. Beauchêne
CIRAD, UMR ECOFOG, ECOlogie des FOrêts de Guyane, Kourou, French Guiana, France

J. Ruelle
INRA, UMR Laboratoire d'Etude des Ressources Forêt-Bois, Champenoux, Nancy, France

E. Nicolini
CIRAD, UMR AMAP, botAnique et bioinforMatique de l'Architecture des Plantes, Montpellier, France

P. Heuret
INRA, UMR ECOFOG, ECOlogie des FOrêts de Guyane, Kourou, French Guiana, France

B. Thibaut
CNRS, UMR Laboratoire de Mécanique et Génie Civil de Montpellier, Montpellier, France

studies (Boninsegna et al. 2009; Pumijumnong 2013). These data are therefore very important to estimate tree age (Worbes et al. 2003; Brienen 2005), to study wood properties (Bouriaud et al. 2005; Franceschini et al. 2013), or more generally, to study forest dynamics (Rozendaal and Zuidema 2011) and carbon storage (Worbes and Raschke 2012).

Tree growth is controlled by both endogenous factors, such as plant genotype or physiological processes (Schrader et al. 2003, 2004), and by exogenous factors, such as rainfalls and light availability (Deslauriers and Morin 2005; Gricar et al. 2007), and these factors affect tree growth in an interrelated way.

In temperate regions, winter conditions influence tree phenology through a synchronized annual period of rest for both primary and secondary growth, which, in deciduous species, is associated with leaf shedding. In this case, climatic conditions are the main factor that controls tree growth dynamics and the long winter-induced rest period leaves markers in the wood and on the stems.

In tropical rainforest, climatic parameters (temperature, light, and rainfall) are less restrictive, and fluctuations in primary and secondary growth can be caused by various environmental factors: rainfall variations (Bullock and Solismagallanes 1990; Wright and Cornejo 1990; Pumijumnong et al. 1995; Worbes 1995; Bullock 1997; Borchert 1999; Worbes 1999; Oliveira et al. 2011; Grogan and Schulze 2012), annual floods (Callado et al. 2001; Schöngart et al. 2002, 2005; Dezzeo et al. 2003), variations in day length (Borchert and Rivera 2001; Williams et al. 2008), variations in peaks of irradiance (ter Steege and Persaud 1991; van Schaik et al. 1993; Wright and van Schaik 1994), and by internal rhythms (Alvim and Alvim 1978). According to these various sources of growth fluctuation, tropical tree species display more diverse growth patterns than temperate ones, from trees exhibiting a continuous growth to trees with intermittent growth (Osada et al. 2012; Zalamea et al. 2013). Thus, the macro-anatomical or morphological growth markers may not correspond to an annual rhythm, or to any period of fixed time, and may even be absent from the wood or stems (Jacoby 1989; Wils et al. 2009; Nicolini et al. 2012). This can be an issue in dendrochronological studies, and it highlights the importance of a better understanding of tropical tree growth periodicity.

Despite many studies, our knowledge on leaf and cambium phenologies of tropical trees remains sparse and there is still no coordinated vision of how these processes interact with each other and with the environment. In South American tropical forests, 15 studies on cambial seasonal activity have been conducted using histological approaches (Callado et al. 2013). Although a period of cambial dormancy appeared to occur during the dry season (Krepkowski et al. 2011; Die et al. 2012), the cambial activity sometimes appears to be independent of seasonality (Trouet et al. 2012; Pumijumnong and Buajan 2013). Concerning leaf phenology, both large-scale continental studies using satellite data (Caldararu et al. 2012; Pennec et al. 2011) and field studies (Loubry 1994; Nicolini et al. 2012) showed that new flush of leaves appeared shortly after leaf fall at the beginning of the dry season, but some species also appeared to have a non-seasonal leaf phenology (Nicolini et al. 2012; Borchert 1999). Finally, the few studies on the relationship between leaf phenology, cambial activity, and environmental variables, showed that cambial activity was reduced during the dry season when the trees were leafless (Callado et al. 2001; Marcati et al. 2006; Venugopal and Liangkuwang 2007; Lisi et al. 2008; Marcati et al. 2008; Yàñez-Espinosa et al. 2010; Singh and Venugopal 2011). However, they rarely focused on species in which the leafless period and the dry season were disconnected in time, which is a necessary condition to disentangle the effect of the dry season and the effect of leaf fall on cambial activity.

In the present study, we thus investigated seasonal variations in cambial activity in tropical trees in relation with their leaf shedding pattern and climatic factors. We focused on two emergent neotropical species: *Parkia nitida* Miq. (Fabaceae) and *Parkia velutina* Benoist (Fabaceae). Both are deciduous and have easily identifiable successive growth rings (Détienne 1989; Nicolini et al. 2012; Morel 2013). *P. nitida* trees exhibit a stable annual and seasonal defoliation pattern (Loubry 1994; Mangenet 2013). In contrast, some *P. velutina* trees also have a stable annual and seasonal defoliation pattern while others showed a stable but infra-annual defoliation pattern, with leaf shedding every 7–10 month, leading to non-seasonal defoliation from year to year (census 1990–1991 in Loubry 1994; census 2009–2011 in Nicolini et al. 2012).

Using these two different species, we attempted to clarify the relationship between cambial activity and leaf phenology to answer the three following questions: (1) is cambial activity seasonal?, (2) are cambial activity and leaf phenology linked?, and (3) are the two processes linked to climate seasonality?

Materials and methods

Study site and tree selection

The study was conducted in the lowland tropical rainforest of the Paracou experimental site at 5°18′N, 52°55′W, French Guiana (Gourlet-Fleury et al. 2004). The site is a stand of old-growth forest dominated by Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae, and Burseraceae

(Sabatier and Prévost 1989). The most common soils are shallow and ferralitic, limited in depth by a more or less transformed loamy saprolite (Boulet and Brunet 1983).

The site receives nearly two-thirds of the annual 3041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month in September and October (Wagner et al. 2011). The daily mean temperature of 25.8 °C is almost constant over the year.

We studied five trees of each of the two species, distributed throughout the Paracou field station. Tree diameters at breast height (DBH) ranged from 45 to 100 cm (Table 1a). Only trees with an emergent crown (full overhead and side light) or that were in the upper canopy layer (full overhead light) were selected to minimize the effects of competition for light on tree growth.

Wood formation monitoring

Wood formation was monitored every 15 days by sampling microcores (15 mm in length and 2 mm in diameter) from the stem of the selected trees. The survey lasted 24 months (February 2010–February 2012) for *P. nitida* and 34 months (April 2009–February 2012) for *P. velutina*. Microcores were collected at breast height using a Trephor tool (Rossi et al. 2006a). Samples were taken in a spiral up the stem from 30 cm below to 30 cm above DBH, 2–8 cm apart (Deslauriers et al. 2003). This spacing is necessary because traumatic tissues may form where previous cores have been removed (Forster et al. 2000). Once sampled, the microcores were conserved in an ethanol solution (50 % in water) in Eppendorf microtubes and stored at 5 °C to avoid tissue deterioration. Some samples were not exploitable (10 % of the microcore data) due to the extreme fragility of microcores, which break easily when handled.

Table 1 (a) Diameters at breast height (DBH) and heights (*H*) of the sampled trees of *Parkia nitida* and *Parkia velutina* and (b) periodicity of leaf fall and cambial activity

	(a)		(b)	
	DBH (cm)	H (m)	Leaf fall periodicity (months)	Cambial activity periodicity (months)
Parkia nitida				
PN1	85.9	30.0	12	11.5
PN2	105.0	27.0	12	9.5
PN3	76.4	26.6	11	13
PN4	47.8	19.5	13	12
PN5	70.0	28.5	12	–
Parkia velutina				
PV1	93.9	34.0	8, 9	7.5
PV2	89.1	32.5	9, 8, 7, 10	14.5
PV3	70.0	31.5	8, 10, 10	10.5
PV4	47.7	31.0	11, 13	12.5
PV5	45.8	31.0	10, 10, 9	11

Leaf fall periodicity is expressed as the length (in months) of the leafy period between two successive leaf falls

For PN5, "–" for cambial activity means no seasonal pattern observed

To allow microscopic observation of cambial activity and wood formation, transverse sections were prepared from every microcore. Each sample was oriented by making a pencil mark on the transversal side under a microscope at 12× magnification. The samples were then dehydrated before being embedded in paraffin. Next, 5 µm transverse sections were cut with a rotary microtome (Leica, RM 2255). Finally, sections were stained with cresyl violet acetate (0.16 % in water) and observed with visible and polarized light at 100× magnification (Rossi et al. 2006a).

We distinguished three distinct cell zones in the sections: (1) a cambial zone (cz) with cells with thin cell walls and small radial diameters, (2) a zone in which the cells were enlarging (ez) where the cells were larger than those in the cambial zone and had thin walls, and (3) a zone in which the cell walls were thickening (wz) where the cells exhibiting birefringence were developing secondary walls under polarized light and appeared violet and blue under white light after staining with cresyl violet acetate (Samuels et al. 2006). The Wiesner reaction was performed on additional sections by pouring a few drops of 2 % phloroglucinol ethanol solution onto the section mounted on a glass slide, adding one drop of 35 % HCl and covering the section with a cover slip. The Wiesner reagent reacts with coniferyl (G) and sinapyl (S) aldehyde units in lignin. The higher the Klason lignin content, the more intense the red color (Yoshizawa et al. 2000). The difference in color makes it possible to differentiate cells with thickening walls from the first mature cells.

To determine cambial activity, we recorded the radial number of cells along three continuous cellular files in each cell zone (Figs. 1, 2; Skene 1969; Antonova et al. 1995; Deslauriers et al. 2003; Rossi et al. 2006b). Despite the fact that these two species are known to have distinct growth rings (Nicolini et al. 2012 for *P. velutina* and Morel 2013 for *P. nitida*), we did not observe growth ring limits in the microcore sections and were thus unable to include mature cells in our counts.

Phenological survey

In addition to wood formation monitoring in the same trees, we used binoculars to assess the vegetative state according to the four following categories: leafless (>80 % crown without leaves), young (>80 % crown with light-green expended leaves), mature (>80 % crown with dark-

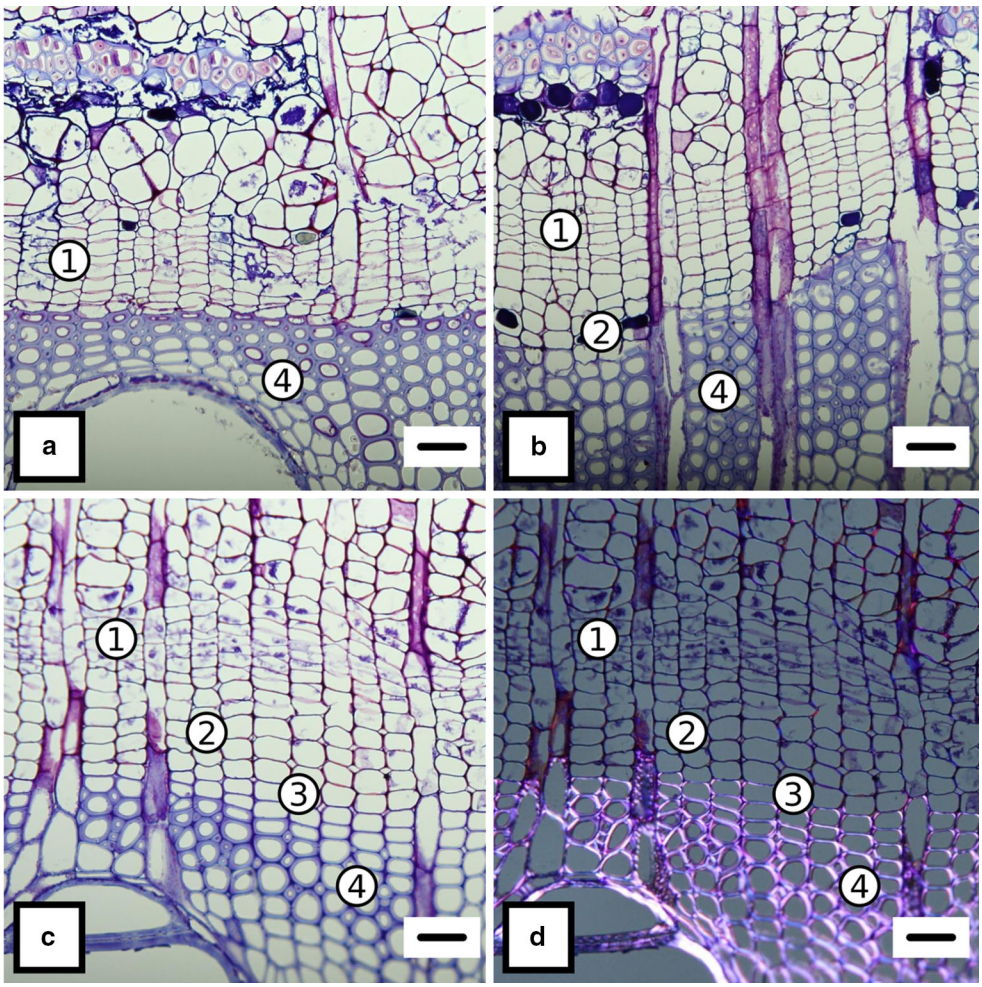

Fig. 1 Cross sections of a *Parkia nitida* stem, **a** period of low cambial activity (May 4, 2010), **b** transition period (July 13, 2010), **c** strong cambial activity, and **d** strong cambial activity in polarized light (December 26, 2011). *1* Cambial zone (cz), *2* zone with enlarging cells (ez), *3* zone with cells with thickening walls (wz), and *4* mature cells. *Scale bars* 25 μm

green leaves), and senescent (>80 % crown with yellow–brown leaves). All observations were made by the same researcher (T.M.), thus minimizing subjective estimation variability.

Data analysis

Concerning climatic variables, after a preliminary analysis (see online supplementary materials for details, Fig. A1), we extracted the four following climatic parameters from each 15-day time window preceding each sampling data: (1) sum precipitation, (2) mean temperature, (3) mean relative humidity, and (4) mean solar radiation. Because climatic parameters were highly interrelated, we chose to summarize the climatic information using a principal component analysis (PCA). The first axis of the PCA explained up to 77 % of the inertia. We used the first axis score as a summary climatic variable because of its significant correlation with each of the climatic parameters (Fig. 3). In this way, we obtained an easy way to interpret climate variable centered on zero in which negative values represented hot dry periods and positive values represented cool moist periods (Fig. 3).

Concerning leaf phenology, the skewed bell-shaped patterns of photosynthetic capacity through a leaf's lifetime (Kuo et al. 2013), along with the fact that the durations of the senescent, defoliation, and young leaf stages were very short when considered separately compared with the duration of the mature leaf stage, lead us to focus on mature leaves versus other stages of leaf phenology in our analysis.

Concerning cambial phenology, we tested periodicity using Spearman's linear correlation coefficient (for more details see online supplementary materials, Fig. B1).

We then explored the relationships between cambial activity, leaf phenology, and climate seasonality using linear mixed models. We chose to explore these relationships separately because both cambial activity and leaf phenology were likely to be sensitive to climate. If we used leaf

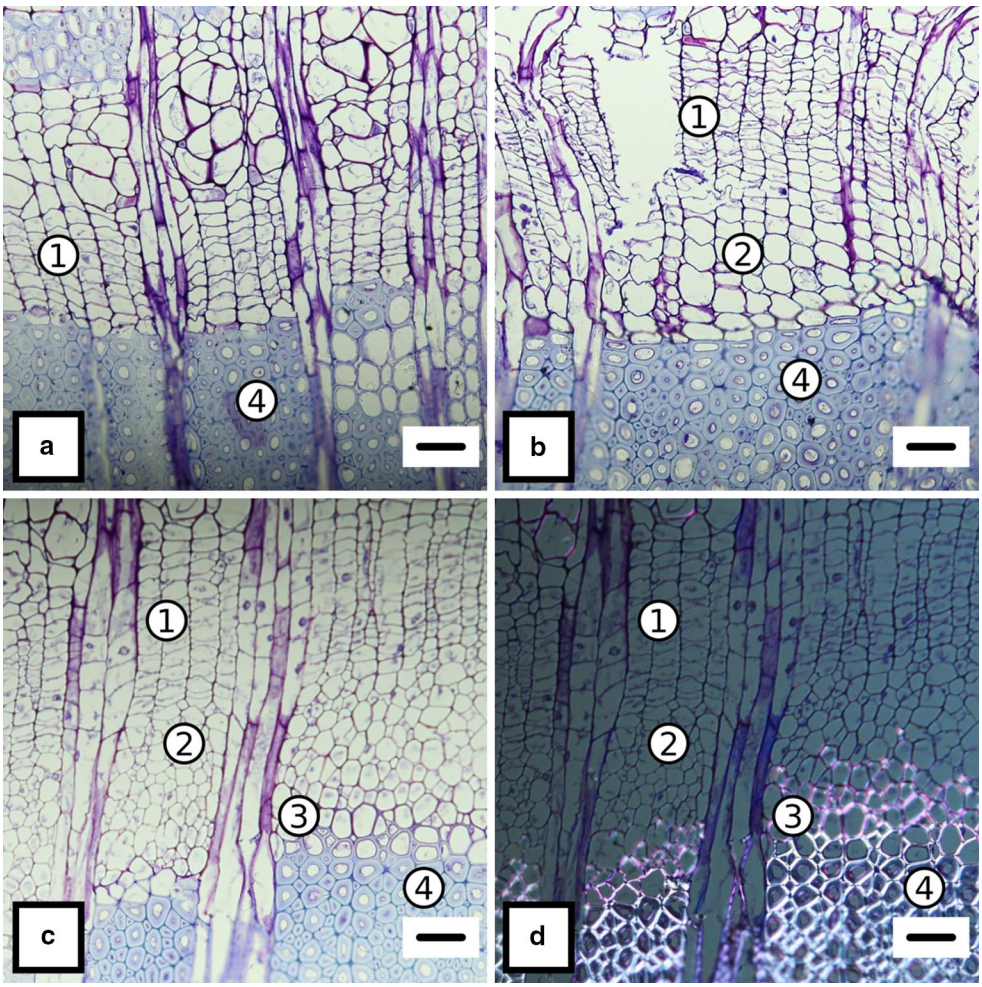

Fig. 2 Cross sections of a *Parkia velutina* stem, **a** reduced cambial activity period (May 4, 2010), **b** transition period (July 27, 2010), **c** high cambial activity, and **d** high cambial activity in polarized light (December 2, 2010). *1* Cambial zone (cz), *2* zone with enlarging cells (ez), *3* zone with cells with thickening walls (wz), and *4* mature cells. *Scale bars* 25 µm

phenology and climate simultaneously in a model to explain variations in cambial activity, we would not be able to distinguish real climatic effects from indirect effects. In order to take into account the inter-individual variability, we integrated in each model an individual random effect on both intercept and slope. Thus, we first explored the relation between cambial activity and climate with a linear mixed model in which we set climate as a fixed variable and individual ranking as random effect on both intercept and slope: (1) cambial activity $\sim$ climate + (1 + climate | individual). We then explored the relation between cambial activity and leaf phenology using a linear mixed model in which we set leaf phenology as a fixed variable and individual ranking as a random effect on both intercept and slope: (2) cambial activity $\sim$ leaf phenology + (1 + leaf phenology | individual). Finally, we explored the relation between leaf phenology and climate using a mixed logistic regression analysis in which we set climate as a fixed variable and individual ranking as a random effect on both intercept and slope: (3) leaf phenology $\sim$ climate + (1 + climate | individual). We log10-transformed cambial activity in models (1) and (2) to obtain more symmetric distributions.

Due to the absence of standard statistical procedures to assess the significance of fixed explicative variables in mixed models, we used a parametric bootstrap approach to compute 95 % confidence intervals for each estimated parameters and we could then infer on the significance of the fixed explicative variables.

For models (1) and (2), we expressed the goodness-of-fit with the marginal R^2 (R^2_m), which gives the variance explained by the fixed variables, and with the conditional R^2 (R^2_c), which gives the variance explained by both fixed and random variables (Nakagawa and Schielzeth 2013). For model (3), we expressed the goodness-of-fit with the area under the receiver operating characteristic (ROC) curve (expressed thereafter as AUC), which represents the

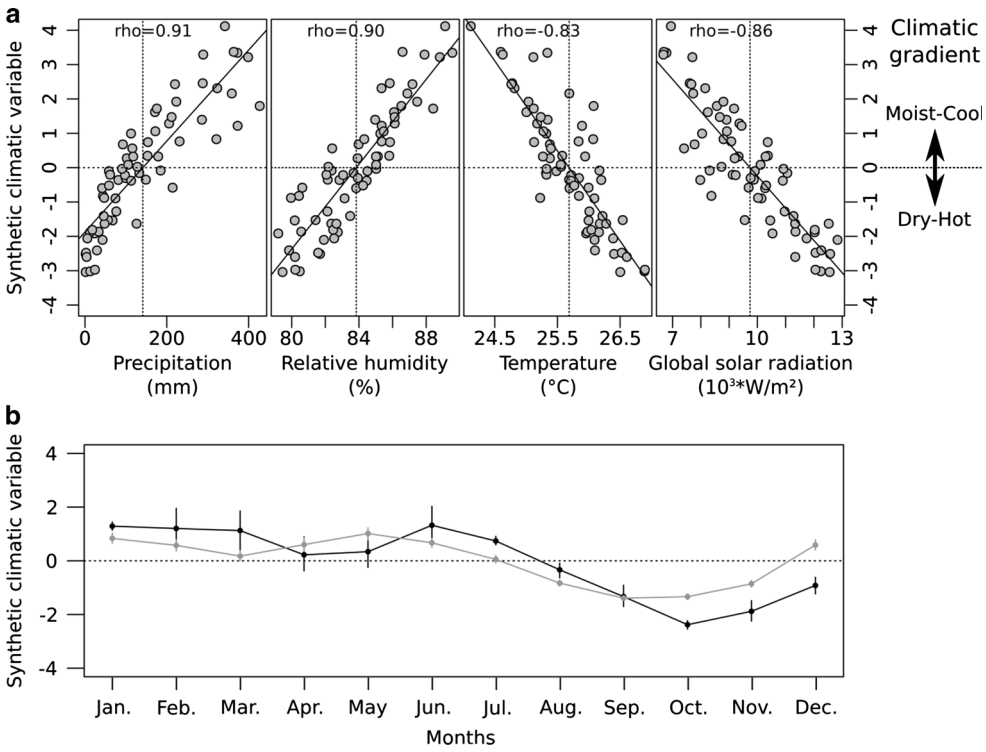

Fig. 3 **a** Correlations between climatic parameters (precipitation, relative humidity, temperature, and global solar radiation) and the summary climate variable. **b** Monthly variation in summary climatic variable during the survey (*black line*) and during the 2004–2012 period (*gray line*). The summary variable is centered on zero. *Negative values* represented dry and hot periods while *positive values* represented rather moist and cool periods. *Bars* represent 95 % bootstrapped confidence intervals. *Rho* Spearman's rank correlation coefficient. Significance levels associated with the Spearman's rank correlation coefficient was $P < 0.001$ in all cases

discriminative ability of the model, i.e.. in our case, the ability of the model to predict tree phenology according to climatic data. AUC can be seen as the proportion of true predictions made by the model, and range from 0.5 (null prediction ability) to 1 (excellent prediction ability).

All analyses were performed using the R statistical platform (R Development Core Team 2011) and the lme4 package (Bates et al. 2014).

Results

Leaf shedding pattern

In 2010 and 2011, all *P. nitida* trees lost their leaves at the same time during the long dry season, at intervals of 11–13 months (Fig. 4; Table 1b). The leafless period lasted 15–30 days.

During the 3 years of the survey, individual *P. velutina* trees went through three to five leafless periods (Fig. 4; Table 1b), implying that some trees lost their leaves twice a year. The leafless period was slightly synchronous between trees, but could occur at any time of the year (Fig. 4). Most trees lost their leaves at sub-annual scale, at intervals from 7 to 10 months (PV1, PV2, PV3, and PV5) and only one tree showed annual defoliation behavior (PV4, Table 1b). Like *P. nitida*, the leafless period lasted 15–30 days.

Cambial activity pattern

Cambial activity varied between the two species and among trees, with each tree alternating in the periods of low and high cambial activity during the survey (Fig. 4). In *P. nitida*, the periodicity of cambial activity was close to annual in PN1, PN3, and PN4, but less than annual in PN2 (Fig. 4; Table 1b). We did not observe any periodicity in PN5, probably due to its very weak cambial activity. In *P. velutina*, cambial activity periodicity ranged from 7.5 to 14.5 months.

In both species, the variation in cambial activity was mainly the result of changes in the number of enlarging cells (ez) and wall-thickening cells (wz) (Fig. 4, green-dashed lines and blue dash-dotted lines), whereas the number of cells in the cambial zone (cz) remained more or less constant over time (Fig. 4, red-dotted lines).

Relationships between cambial activity, leaf phenology, and climate

In both species, cambial activity at the population scale tended to increase from hot and dry periods to moist and cool periods, but this trend was not significant (Table 2; Fig. 5a, b). The result was reinforced by the fact that we observed individual trees showing an opposite trend in the relationship between cambial activity and climate in both species (Fig. 5a, b).

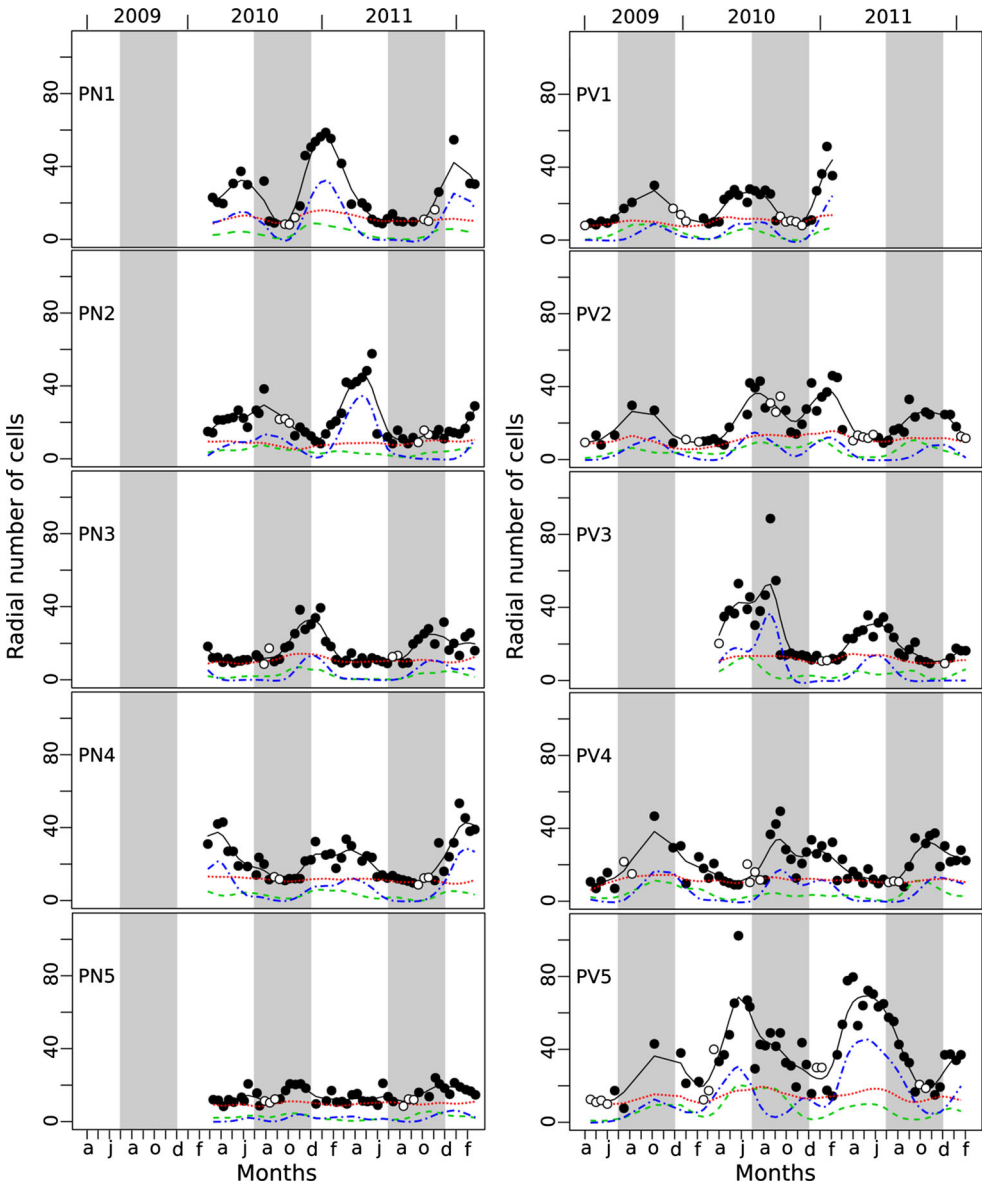

Fig. 4 Cambial activity and leaf shedding patterns of the five *Parkia nitida* (*on the left*) and of the five *P. velutina* trees (*on the right*) from April 2009 to February 2012. The *red-dotted*, *green-dashed,* and the *blue dash-dotted lines* represent, respectively the number of cell layers of the cambial zone (cz), of the zone with enlarging cells (ez) and of the zone with cells with thickening walls (wz), while the *circles* represent the sum of these three measurements (Σ_cz_ez_wz) and the local fitting is represented by the *solid line*. The *color of the circles* indicates the phenological stage of the tree at the time of the microcore sampling: *black* for "mature leaves" and *white* for "senescent leaves", "leafless", and "young leaves". The long dry season (July–November) is symbolized by the *gray stripes* in the background

On the other hand, we found a positive and statistically significant increase of cambial associated with the presence of mature leaves at the population scale in both species (Table 2; Fig. 5b, c), and this increase in cambial activity was observed in all individuals. Cambial activity tended to decrease before leaf fall and to increase again immediately or with a lag of a few months after canopy leafing (Fig. 4).

Finally, while the presence of mature leaves was significantly related to cool moist periods in *P. nitida*, no significant link between climate and leaf phenology at the population scale was observed for *P. velutina*. In only one tree out of the five of this species, the probability of observing mature leaves increased significantly from the hot and dry to the moist and cool periods.

Discussion

The present work is original, in that it is among the very few studies on tropical trees to explore cambial activity through regular sampling of microcores at a bi-monthly scale (see Callado et al. 2013 for a review of studies in South America). Importantly, we included leaf phenology as an additional biological covariable because it reflected the functioning of the primary meristems while most other studies focused only on cambial activity and its links with environmental factors, sometimes on the radial increment alone (Callado et al. 2013). In our opinion, cambial activity plus leaf phenology definitely offer a larger insight on the growth regulation occurring inside the growing plant and

Table 2 Summaries of the linear mixed model analyses of relationships between cambial activity and climate (model 1), and cambial activity and leaf phenology (model 2), the mixed logistic regression model analyses of relationships between phenology and climate (model 3) for *Parkia nitida* and *Parkia velutina*

Parkia nitida		*Parkia velutina*	
Model (1) ln(cambial activity) ~ intercept + climate + (intercept + climate | individual)			
Fixed effects	Coefficient [95 % CI]	*Fixed effects*	Coefficient [95 % CI]
Intercept β_0	2.85 [2.70; 2.99]	Intercept β_0	3.02 [2.77; 3.27]
Climate β_1	0.04 [–0.04; 0.12]	Climate β_1	0.04 [–0.04; 0.11]
Individual random effects	SD	*Individual random effects*	SD
Intercept β_0	0.16	Intercept β_0	0.26
Climate β_1	0.08	Climate β_1	0.08
Goodness-of-fit		*Goodness-of-fit*	
Marginal R^2	0.02	Marginal R^2	0.01
Conditional R^2	0.21	Conditional R^2	0.24
Model (2) ln(cambial activity) ~ intercept + phenology + (intercept + phenology | individual)			
Fixed effects	Coefficient [95 % CI]	*Fixed effects*	Coefficient [95 % CI]
Intercept β_0	2.51 [2.33; 2.68]	Intercept β_0	2.61 [2.42; 2.81]
Phenology β_1	0.38 [0.14; 0.34]	Phenology β_1	0.49 [0.30; 0.71]
Individual random effects	SD	*Individual random effects*	SD
Intercept β_0	0.01	Intercept β_0	0.15
Phenology β_1	0.19	Phenology β_1	0.13
Goodness-of-fit		*Goodness-of-fit*	
Marginal R^2	0.06	Marginal R^2	0.10
Conditional R^2	0.17	Conditional R^2	0.29
Model (3) phenology ~ intercept + climate + (intercept + climate | individual)			
Fixed effects	Coefficient [95 % CI]	*Fixed effects*	Coefficient [95 % CI]
Intercept β_0	2.87 [2.21; 4.34]	Intercept β_0	1.54 [1.21; 1.98]
Climate β_1	0.80 [0.31; 1.51]	Climate β_1	0.06 [-0.16; 0.31]
Individual random effects	SD	*Individual random effects*	SD
Intercept β_0	0.47	Intercept β_0	0.20
Climate β_1	0.43	Climate β_1	0.16
Goodness-of-fit		*Goodness-of-fit*	
AUC	0.82	AUC	0.63

Cambial activity was log10-transformed in model (1) and (2). Fixed effects indicate the model estimated parameters at the population scale while taking into account the inter-individual variability. Random effects provide information concerning the inter-individual source of variability (expressed as standard deviation) of the model estimated parameters. The significance of relationships can be inferred from the 95 % parametric bootstrap confidence intervals. The marginal R^2 gives the variance explained by the fixed effects and the conditional R^2 gives the variance explained by both fixed and random effects. *AUC* represent the ability of the model to predict tree phenology according to climatic data and range from 0.5 (null prediction ability) to 1 (perfect prediction ability). See the data analysis section for more details

on the possible interactions with exogenous parameters like temperature or precipitation.

In both species, the variation in cambial activity was mainly the result of changes in the number of enlarging and wall-thickening cells rather than changes in the number of cells in the cambial zone. While the majority of studies on cambial activity in both temperate and tropical trees only focused on the number of cells in the cambial zone to explain cambial activity (temperate studies: Bäucker et al. 1998; Frankenstein et al. 2005; Marion et al. 2007, tropical studies: Pumijumnong and Wanyaphet 2006; Marcati et al. 2008; Krepkowski et al. 2011; Die et al. 2012; Pumijumnong and Buajan 2013); our results show that the other types of cells should also be taken into account in the analysis of cambial activity in tropical trees. Indeed, variations in the number of cells in the cambial zone can be significantly smaller than variations in the number of other cell types.

Despite the fact these two species are known to have distinct growth rings (Nicolini et al. 2012 for *P. velutina*, Morel 2013 for *P. nitida*), we were unable to distinguish the limits of the growth rings in the microcores due to (1) the small size of the core and (2) the confusion between the bands of axial parenchyma lines located within the ring and the continuous band of axial parenchyma corresponding to

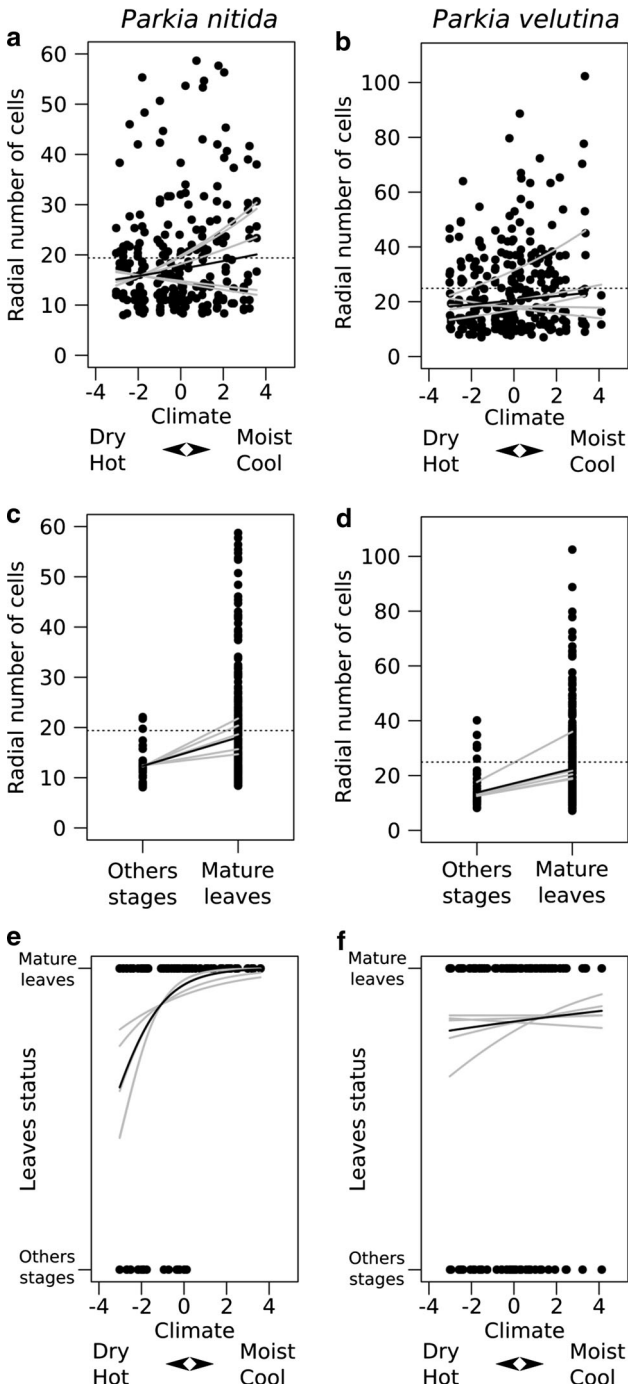

Fig. 5 Relationships between leaf phenology, cambial activity and climate seasonality at population scale in *Parkia nitida* (**a**, **c**, and **e**) and *Parkia velutina* (**b**, **d,** and **f**). The *black curves* represent the mixed model predictions for the fixed effect at the population scale and the *gray curves* represent the mixed model individual predictions. The *circles* represent the actual observations. In **a**, **b**, **c**, and **d**, the *horizontal striped line* corresponds to the mean cambial activity during the survey at population scale. In **a**, **b**, **e,** and **f**, the *x*-axis corresponded to synthetic climate variable centered on zero (obtained with a PCA on climatic variables). *Negative values* represented hot dry periods and *positive values* represented cool moist period

the end of the current ring. Consequently, we were unable to take the mature cells into account in our counting and thus, to obtain other cambial activity parameters like the speed of differentiation of the cells, a parameter indicative of tree growth status was introduced. Future studies should include longer cores but at a monthly scale to prevent disease entrance.

The main result of this study was that periods of low cambial activity significantly matched with leaf fall and leafless periods in both species, and this result was reported in several others studies in deciduous and semi-deciduous tree species (Callado et al. 2001; Venugopal and Liangkuwang 2007; Marcati et al. 2008; Cardoso et al. 2012). Leaf phenology is known to be an important factor influencing the activity of the vascular cambium and leaf fall generally has a significant and direct effect on cambial activity, as reported by Callado et al. (2001) where the period of leaf abscission was correlated with the formation of latewood in three deciduous and semi-deciduous species. Thus, it's clear that the radial growth cannot be considered and interpreted in deciduous and semi-deciduous species without taking into account the leaf phenology in studies about effects of climate on tree radial growth.

Leaf shedding patterns are largely determined by the seasonality of rainfall in tropical regions (Frankie et al. 1974; Lieberman 1982; Reich and Borchert 1982, 1984; van Schaik et al. 1993; Lisi et al. 2008). To avoid hydric stress, deciduous trees that shed their leaves at the beginning of the dry season, remain leafless throughout the dry season and only grow new leaves when the first rains fall at the end of the dry season. Conversely, in the Paracou experimental site, *P. nitida* trees change their leaves early in the dry season, just before depletion of soil water reserves (Wagner et al. 2011), and end the dry season with new leaves (see also trees observed by Loubry 1994, Pennec et al. 2011 and Mangenet 2013). The dry season is characterized by a minimum cloud cover and high solar irradiation, a situation that probably allows trees to optimize their photosynthetic activity (Wright and van Schaik 1994; Huete et al. 2006; Xiao et al. 2006).

However, Mangenet (2013) reports that some *P. nitida* trees (3 of 14 trees) changed their leaves during other periods than long dry season, suggesting that sensibility to climate could be unequal between individuals, a well-observed point for *P. velutina*. Thus, the variability of the leaf life span we observed in *P. velutina*, combined with its apparent non-seasonal and non-annual leaf fall behavior, suggest that they were not only influenced by climate factors (e.g., occurrence of the dry season which is supposed to influence all trees equally). This hypothesis is supported by similar observations in other tropical studies (Lieberman 1982; Reich and Borchert 1982; van Schaik et al. 1993; Do

et al. 2005; Singh and Kushwaha 2005; Elliott et al. 2006; Yàñez-Espinosa et al. 2006; Williams et al. 2008; Valdez-Hernández et al. 2010; Mendez-Alonzo et al. 2013).

Contrary to *P. nitida* and even if trees grew in the same conditions, both leaf fall periodicity and cambial activity were variable in *P. velutina* in our study. However, we can also observe in *P. nitida* leaf fall pattern variability as shown by Nicolini et al. (2012) and Mangenet (2013). So, this variability necessarily involves the influence of other factors than the seasonality of the precipitation alone, such as soil and microclimatic conditions (Reich and Borchert 1982; Singh and Kushwaha 2005; Valdez-Hernández et al. 2010; Cardoso et al. 2012) or physiological factors like internal clock (Yàñez-Espinosa et al. 2006; Williams et al. 2008; Lüttge and Hertel 2009; Seyoum et al. 2012). For example, Brousseau et al. (2013) showed the existence of an individual variability of the leaves' photosynthetic efficiency that could allow the faster realization of the foliar phenological cycle which could be a rational explanatory factor of the variation of the length cycle.

In conclusion, this study highlighted the interrelations between leaf phenology, cambium phenology, and climate in two closely related tropical tree species in French Guiana. For *P. nitida*, the cambial activity pattern was seasonal, annual, and synchronous at the population scale whereas it was non-seasonal, non-annual, and asynchronous in *P. velutina* but periodic at the tree scale. In spite of these differences, we found that the periods of cambial inactivity were significantly associated with leaf fall and leafless stages in both species. Further studies will be necessary to examine possible connections between plant ontogeny and patterns of leaf phenology and cambial activity and disentangle their interrelated relationships.

Author contribution statement HM, TM, JR, and JB helped to the data acquisition. HM, TM, and PH participated in the data analysis. HM, TM, JR, JB, PH, EN, and BT contributed to the writing of this paper.

Acknowledgments We are grateful to CIRAD, Dendrotropic, and Guyaflux. We also thank Maryline Harroué and Cyrille Rathgeber for allowing us to use their technical facilities (Xylosciences platform, LERFOB) for the embedding and inclusion processes and for sharing their knowledge about cambial activity. H. Morel received an assistantship from CNES (50 %) and FSE (50 %).

Conflict of interest The authors declare that they have no conflict of interest.

References

Alvim PT, Alvim R (1978) Relation of climate to growth periodicity in tropical trees. In: Zimmermann MH (ed) Tomlinson PB. Tropical trees as living systems Cambridge University Press, London, pp 445–464

Antonova GF, Cherkashin VP, Stasova VV, Varaksina TN (1995) Daily dynamics in xylem cell radial growth of Scots Pine (*Pinus sylvestris* L.). Trees 10:24–30

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–7

Bäucker E, Bues CT, Vogel M (1998) Radial growth dynamics of spruce (*Picea abies*) measured by micro-cores. IAWA J 19:301–309

Boninsegna JA, Argollo J, Aravena JC, Barichivich J, Christie D, Ferrero ME, Lara A, Le Quesne C, Luckman BH, Masiokas M, Morales M, Oliveira JM, Roig F, Srur A, Villalba R (2009) Dendroclimatological reconstructions in South America: a review. Palaeogeogr Palaeocl 281:210–228

Borchert R (1999) Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. IAWA J 20:239–247

Borchert R, Rivera G (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. Tree Physiol 21:213–221

Boulet R, Brunet D (1983) Prospection pédologique en vue de l'implantation des blocs de l'opération CTFT "Forêt Naturelle".Technical report. ORSTOM, Cayenne, p 7

Bouriaud O, Leban JM, Bert D, Deleuze C (2005) Intra-annual variations in climate influence growth and wood density of Norway spruce. Tree Physiol 25:651–660

Brienen RJW (2005) Tree rings in the tropics: a study on growth and ages of Bolivian rain forest trees. Dissertation, University of Utrecht

Brousseau L, Bonal D, Cigna J, Scotti I (2013) Highly local environmental variability promotes intrapopulation divergence of quantitative traits: an example from tropical rain forest trees. Ann Bot 112(6):1169–1179

Bullock SH (1997) Effects of seasonal rainfall on radial growth in two tropical tree species. Int J Biometeorol 41:13–16

Bullock SH, Solismagallanes JA (1990) Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 22:22–35

Caldararu S, Palmer PI, Purves DW (2012) Inferring Amazon leaf demography from satellite observations of leaf area index. Biogeosciences 9:1389–1404

Callado CH, Neto SJD, Scarano FR, Costa CG (2001) Periodicity of growth rings in some flood-prone trees of the Atlantic Rain Forest in Rio de Janeiro, Brazil. Trees 15:492–497

Callado CH, Roig FA, Tomazello-Filho M, Barros CF (2013) Cambial growth periodicity studies of South American woody species—a review. IAWA J 34:213–230

Cardoso FCG, Marques R, Botosso PC, Marques MCM (2012) Stem growth and phenology of two tropical trees in contrasting soil conditions. Plant Soil 354:269–281

Deslauriers A, Morin H (2005) Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. Trees 19:402–408

Deslauriers A, Morin H, Begin Y (2003) Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada). Can J For Res 33:190–200

Détienne P (1989) Appearance and periodicity of growth rings in some tropical woods. IAWA J 10:123–132

Dezzeo N, Worbes M, Ishii I, Herrera R (2003) Annual tree rings revealed by radiocarbon dating in seasonally flooded forest of the Mapire River, a tributary of the lower Orinoco River, Venezuela. Plant Ecol 168:165–175

Die A, Kitin P, Kouame FN, Van den Bulcke J, Van Acker J, Beeckman H (2012) Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (*Tectona grandis*) in Ivory Coast. Ann Bot 110:861–873

Do FC, Goudiaby VA, Gimenez O, Diagne AL, Diouf M, Rocheteau A, Akpo LE (2005) Environmental influence on canopy phenology in the dry tropics. Forest Ecol Manag 215:319–328

Elliott S, Baker PJ, Borchert R (2006) Leaf flushing during the dry season: the paradox of Asian monsoon forests. Global Ecol Biogeogr 15:248–257

Forster T, Schweingruber FH, Denneler B (2000) Increment puncher —a tool for extracting small cores of wood and bark from living trees. IAWA J 21:169–180

Franceschini T, Longuetaud F, Bontemps JD, Bouriaud O, Caritey BD, Leban JM (2013) Effect of ring width, cambial age, and climatic variables on the within-ring wood density profile of Norway spruce *Picea abies* (L.) Karst. Trees 27:913–925

Frankenstein C, Eckstein D, Schmitt U (2005) The onset of cambium activity—a matter of agreement? Dendrochronologia 23:57–62

Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J Ecol 62:881–919

Gourlet-Fleury S, Guehl JM, Laroussinie O (2004) Ecology and management of a neotropical rainforest—lessons drawn from Paracou, a long-term experimental research site in French Guiana. Elsevier, Paris

Gricar J, Zupancic M, Cufar K, Oven P (2007) Regular cambial activity and xylem and phloem formation in locally heated and cooled stem portions of Norway spruce. Wood Sci Technol 41:463–475

Grogan J, Schulze M (2012) The impact of annual and seasonal rainfall patterns on growth and phenology of emergent tree species in southeastern Amazonia, Brazil. Biotropica 44:331–340

Huete AR, Didan K, Shimabukuro YE, Ratana P, Saleska SR, Hutyra LR, Yang WZ, Nemani RR, Myneni R (2006) Amazon rainforests green-up with sunlight in dry season. Geophys Res Lett 33:1–4

Jacoby GC (1989) Overview of tree ring analysis in tropical regions. IAWA Bull 10:99–108

Krepkowski J, Bräuning A, Gebrekirstos A, Strobl S (2011) Cambial growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. Trees 25:59–70

Kuo Y-L, Huang M-K, Yang Y-L (2013) Dynamic variations in the photosynthetic capacity in a leaf's lifetime for five Taiwanese tree species at different successional stages Taiwan J For Sci 28:17–28

Lieberman D (1982) Seasonality and phenology in a dry forest in Ghana. J Ecol 70:791–806

Lisi CS, Tomazello M, Botoss PC, Roig FA, Maria VRB et al (2008) Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in southeast Brazil. IAWA J 29:189–207

Loubry D (1994) Phenology of deciduous trees in a French-Guianan forest (5 degrees latitude north)—case of a determinism with endogenous and exogenous components. Can J Bot 72:1843–1857

Lüttge U, Hertel B (2009) Diurnal and annual rhythms in trees. Trees 23:683–700

Mangenet T (2013) Approche rétrospective des cycles phénologiques chez quelques espèces guyanaises. Vers une nouvelle branche de la dendrochronologie. Diploma thesis, University of Montpellier

Marcati CR, Angyalossy V, Evert RF (2006) Seasonal variation in wood formation of *Cedrela fissilis* (Meliaceae). IAWA J 27:199–211

Marcati CR, Milanez CRD, Machado SR (2008) Seasonal development of secondary xylem and phloem in *Schizolobium parahyba* (Vell.) Blake (Leguminosae : Caesalpinioideae). Trees 22:3–12

Marion L, Gricar J, Oven P (2007) Wood formation in urban Norway maple trees studied by the micro-coring method. Dendrochronologia 25:97–102

Mendez-Alonzo R, Pineda-Garcia F, Paz H, Rosell JA, Olson ME (2013) Leaf phenology is associated with soil water availability and xylem traits in a tropical dry forest. Trees 27:745–754

Morel H (2013) Dynamique de croissance radiale saisonnière et annuelle des arbres en forêt tropicale humide guyanaise. Diploma thesis, University of Antilles-Guyane

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Nicolini E, Beauchene J, Leudet de la Vallée B, Ruelle J, Mangenet T, Heuret P (2012) Dating branch growth units in a tropical tree using morphological and anatomical markers: the case of *Parkia velutina* Benoist (Mimosoïdeae). Ann For Sci 69:543–555

Oliveira BRU, Latorraca JVD, Tomazello M, Garcia RA, de Carvalho AM (2011) Dendroclimatology correlations of *Eucalyptus grandis* Hill ex Maiden of Rio Claro, RJ State—Brazil. Ciencia Florestal 21:499–508

Osada N, Tokuchi N, Takeda H (2012) Continuous and fluctuating leaf phenology of adults and seedlings of a shade-tolerant emergent tree, *Dipterocarpus sublamellatus*, in Malaysia. Biotropica 44:618–626

Pennec A, Gond V, Sabatier D (2011) Tropical forest phenology in French Guiana from MODIS time series. Remote Sens Lett 2:337–345

Pumijumnong N (2013) Dendrochronology in Southeast Asia. Trees 27:343–358

Pumijumnong N, Buajan S (2013) Seasonal cambial activity of five tropical tree species in central Thailand. Trees 27:409–417

Pumijumnong N, Wanyaphet T (2006) Seasonal cambial activity and tree-ring formation of *Pinus kesiya* in northern Thailand in dependence on climate. Forest Ecol Manag 226:279–289

Pumijumnong N, Eckstein D, Sass U (1995) Tree-ring research on *Tectona grandis* on northern Thailand. IAWA J 16:385–392

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reich PB, Borchert R (1982) Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). Ecology 63:294–299

Reich PB, Borchert R (1984) Water-stress and tree phenology in a tropical dry forest in the lowlands of Costa-Rica. J Ecol 72:61–74

Rossi S, Anfodillo T, Menardi R (2006a) Trephor: a new tool for sampling microcores from tree stems. IAWA J 27:89–97

Rossi S, Deslauriers A, Anfodillo T (2006b) Assessment of cambial activity and xylogenesis by microsampling tree species: an example at the alpine timberline. IAWA J 27:383–394

Rozendaal DMA, Zuidema PA (2011) Dendroecology in the tropics: a review. Trees 25:3–16

Sabatier D, Prévost MF (1989) Quelques données sur la composition floristique et la diversité des peuplements forestiers. Bois et forêts des tropiques 219:31–55

Samuels AL, Kaneda M, Rensing KH (2006) The cell biology of wood formation: from cambial divisions to mature secondary xylem. Can J Bot 84:631–639

Schöngart J, Piedade MTF, Ludwigshausen S, Horna V, Worbes M (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. J Trop Ecol 18:581–597

Schöngart J, Piedade MTF, Wittmann F, Junk WJ, Worbes M (2005) Wood growth patterns of *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. Oecologia 145:454–461

Schrader J, Baba K, May ST, Palme K, Bennett M, Bhalerao RP, Sandberg G (2003) Polar auxin transport in the wood-forming tissues of hybrid aspen is under simultaneous control of

developmental and environmental signals. P Natl Acad Sci USA 100:10096–10101

Schrader J, Nilsson J, Mellerowicz E, Berglund A, Nilsson P, Hertzberg M, Sandberg G (2004) A high-resolution transcript profile across the wood-forming meristem of poplar identifies potential regulators of cambial stem cell identity. Plant Cell 16:2278–2292

Seyoum Y, Fetene M, Strobl S, Beck E (2012) Foliage dynamics, leaf traits, and growth of coexisting evergreen and deciduous trees in a tropical montane forest in Ethiopia. Trees 26:1495–1512

Singh KP, Kushwaha CP (2005) Emerging paradigms of tree phenology in dry tropics. Curr Sci 89:964–975

Singh ND, Venugopal N (2011) Cambial activity and annual rhythm of xylem production of *Pinus kesiya* Royle ex. Gordon (Pinaceae) in relation to phenology and climatic factors growing in sub-tropical wet forest of north east India. Flora 206:198–204

Skene DS (1969) Period of time taken by cambial derivatives to grow and differentiate into tracheids in *Pinus radiata*. Ann Bot 33:253–262

ter Steege H, Persaud CA (1991) The phenology of Guyanese timber species: a compilation of a century of observations. Vegetatio 95:177–198

Trouet V, Mukelabai M, Verheyden A, Beeckman H (2012) Cambial growth season of brevi-deciduous *Brachystegia spiciformis* trees from south central Africa restricted to less than four months. PLoS One 7:1–9

Valdez-Hernández M, Andrade JL, Jackson PC, Rebolledo-Vieyra M (2010) Phenology of five tree species of a tropical dry forest in Yucatan, Mexico: effects of environmental and physiological factors. Plant Soil 329:155–171

van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests - Adaptative significance and consequence for primary consumers. Ann Rev Ecol Syst 24:353–377

Venugopal N, Liangkuwang MG (2007) Cambial activity and annual rhythm of xylem production of elephant apple tree (*Dillenia indica* Linn.) in relation to phenology and climatic factor growing in sub-tropical wet forest of northeast India. Trees 21:101–110

Wagner F, Hérault B, Stahl C, Bonal D, Rossi V (2011) Modeling water availability for trees in tropical forests. Agr Forest Meteorol 151:1202–1213

Williams LJ, Bunyavejchewin S, Baker PJ (2008) Deciduousness in a seasonal tropical forest in western Thailand: interannual and intraspecific variation in timing, duration and environmental cues. Oecologia 155:571–582

Wils THG, Robertson I, Eshetu Z, Sass-Klaassen UGW, Koprowski M (2009) Periodicity of growth rings in *Juniperus procera* from Ethiopia inferred from crosSDating and radiocarbon dating. Dendrochronologia 27:45–58

Worbes M (1995) How to measure growth dynamics in tropical trees: a review. IAWA J 16(4):337–351

Worbes M (1999) Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo forest reserve in Venezuela. J Ecol 87:391–403

Worbes A, Raschke N (2012) Carbon allocation in a Costa Rican dry forest derived from tree ring analysis. Dendrochronologia 30:231–238

Worbes A, Staschel R, Roloff A, Junk WJ (2003) Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. Forest Ecol Manag 173:105–123

Wright SJ, Cornejo FH (1990) Seasonal drought and leaf fall in a tropical forest. Ecology 71:1165–1175

Wright SJ, van Schaik CP (1994) Light and the phenology of tropical trees. Am Nat 143:192–199

Xiao XM, Hagen S, Zhang QY, Keller M, Moore B (2006) Detecting leaf phenology of seasonally moist tropical forests in South America with multi-temporal MODIS images. Remote Sens Environ 103:465–473

Yàñez-Espinosa L, Terrazas T, Lopez-Mata L (2006) Integrated analysis of tropical trees growth: a multivariate approach. Ann Bot 98:637–645

Yàñez-Espinosa L, Terrazas T, Lopez-Mata L (2010) Phenology and radial stem growth periodicity in evergreen subtropical rainforest trees. IAWA J 31:293–307

Yoshizawa N, Inami A, Miyake S, Ishiguri F, Yokota S (2000) Anatomy and lignin distribution of reaction wood in two *Magnolia* species. Wood Sci Technol 34:183–196

Zalamea PC, Sarmiento C, Stevenson PR, Rodriguez M, Nicolini E, Heuret P (2013) Effect of rainfall seasonality on the growth of *Cecropia sciadophylla*: intra-annual variation in leaf production and node length. J Trop Ecol 29:361–365